OTKA Final Report 73597 K
Biomechanical constraints in the structure and function of the noctuid genitalia

Summary of activities and main results

Main activities during the project

- Revision of materials of several internationally important European collections (Berlin, Bonn, Budapest, London, Munich, Vienna), photographic documentation of comprehensive type materials.
- Preparation of about 1800 new genitalia slides
- Electronic storage and database organisation of about 6000 genitalia slides
- Publication or submission of 4 generic revisions
- Submission of a comprehensive paper on the architecture, structural constraints and dyssymmetrisation of external genitalia of Noctuidae
- Preparation of an other review paper on the „lock-and-key" structures of inner genitalia and a paper on the SEM surveys on male antennae
- Publication of two monographic books (in English; Budapest and Copenhagen)
- Talks at international scientific conferences.

This activity was based on the collection of the Hungarian Natural History Museum, Budapest (which is one of the most important and representative Noctuidae collection all over Europe), and several other large museum (see above) and private collections as well. We produced a unique genitalia slide collection of over 15,000 slides (Natural History Museum, Budapest and Dept. of Evolutionary Zoology, University of Debrecen). We have surveyed the genital slide collections of Natural History Museum London; Zoological Research Institute and Museum A. Koenig, Bonn; Zoological State Collection, Münich; Natural History Museum, Paris; Natural History Museum, Vienna (more than 30,000 slides!), prepared several thousands of drawings and photos documenting the genitalia of the studied specimens; most of them are already available in electronical form, too. Hundreds of preparates and SEM photographs of antennae of Noctuidae have been made. The method of survey, therefore, is basically classical taxonomic, but using all modern facilities.

Survey of homologous structures in genitalia, evolutionary trends

By these surveys we recognised several homologous structures in the genital structures of the Noctuidae focusing onto the following structures and processes:

- We described several correlative homologous structures as components of supraspecific architecture of genitalia e.g. in the Noctuinae: *Chersotis-Rhyacia-Epipsilia* suggested monophylum including its numerous species groups (several morphological details have already been published in earlier books and publications: Fibiger, 1993; 1997; Varga, 1998; Varga & Ronkay, 1996), further results in our recent books and revisional papers (Ronkay *et al.* 2009 a,b,c; Zilli *et al.* 2009; Ronkay *et al.* 2010; Varga 2011; Varga & Ronkay 2011). Translocation and fusion of structures, connected with some functional changes, as the modification and transformation of the clavus-juxta complex, with parallel functional solutions in different trifine Noctuidae groups; e.g. *Diarsia*, *Agrochola*, *Amphipoea*, *Abrostola*, *Thysanoplusia*, *Ctenoplusia*, etc. (important morphological details are already published in earlier books and publications: Behounek & Ronkay 1999; Behounek et al. 2010; Ronkay & Varga 1998; Ronkay & Varga 1999; Ronkay et al. 2001;

Varga 1996; 1998; Varga & Gyulai 2001; Varga & Ronkay 2007); these evolutionary processes and their results have been analysed in two comprehensive papers (Varga & Ronkay 2011; mscr.).

- We described the geometry of the three-point fixation (the "seat belt"-principle) in the external genitalia of the *Eugnorisma-Eugraphe-Goniographa* complex, the nested structures of "small and large triangles" in the uncus and valvae with processi, often covered by specialised surface structures (morphological details see: Ronkay & Varga 1999; Varga & Ronkay 1987; 2002; Varga et al. 1990). The results of these studies were first presented by Varga (talk at the 16. European Congress of Lepidopterology, Cluj-Kolozsvár 2009), subsequently in a review paper (Varga & Ronkay 2011).
- Male external genitalia have originally a bilaterally symmetric structure. The bilateral valvae (gonopods) often show a secondary, derived asymmetry, i.e. dyssymmetry. Dyssymmetrisation of homologous structures is regularly connected with some functional changes, with enhancing the clasping and stimulating function of saccular extensions (Ronkay & Varga 1998; Varga 1974; Varga & Ronkay 1991), often combined with the reduction of the free arm of harpe (called "clasper" or later as "ampulla" by Lafontaine and Fibiger). Our new results are presented in Varga & Ronkay (2011) and Varga et al. (in prep.).
- We unravelled some phylogenetic and biogeographic patterns in the process of dyssymmetrisation, its significance of species diversity, surveyed mostly on examples from the subfamilies Hadeninae (Poliina and Discestrina subtribes) and Plusiinae (*Macdunnoughia* and related genera). Results are published in a monographic book (Ronkay et al. 2010) and in a review paper (Varga & Ronkay 2011).
- We also confirmed the effectivity of the "three-point-fixation" principle in the inner genitalia:
  (i) carina – subbasal diverticulum with cornutus – subterminal diverticulum with or without fasciculate cornuti (in *Diarsia*, shown by Varga & Ronkay 2007).
  (ii) carina + T shaped vesica (Hadenini: *Sideritis*, *Conisania*; Apameini: *Apamea* etc.; details and taxonomic analysis are published in the monographic book Zilli et al. 2010).
- Structural parsimony in external vs. internal genitalia of Noctuidae: simplification of male external genitalia combined with sophisticated forms of vesica and co-evolved "lock-and-key" structures: (i) Noctuinae: Chersotis, (ii) Hadenini, Poliina: Ctenoceratoda. Results presented by Varga (talk at the 16. European Congress of Lepidopterology, Cluj-Kolozsvár 2009).

Taxonomic results of the project – monographs and revisions

The main results of the project are two monographic books (unfortunately, three already published volumes of the same series cannot be considered as results of this project). The Volume 3 of this series (and the Vol. 5 under preparation) were also presented at the 16th European Congress of Lepidopterology (Cluj-Kolozsvár) and IX. European Congress of Entomology, together with the 12. Vol. of the series of Noctuidae Europaeae. The volumes 1-4 of the book series: Taxonomic Atlas of Eurasian and North African Noctuidae treat 466 species of 36 genera with illustrations of 5500 specimens and 1300 genitalia slides.
Our Palaearctic Noctuidae database consists of in its recent stage the data and pictures of about 3500 species of 802 genera, and genitalia photos of about 2400 species of 591 genera.

Apamea and related genera belong to the most diverse group of Holarctic trifine Noctuidae. In the monographic book 6 new genera, 7 new subgenera and 29 new species have been described. The main phylogenetic/biogeographic results of this monography are as follows.

Apamea and the closely related genera show several synapomorphies in male and female genitalia. Most important trend is the transformation of the plesiomorphic tubular vesica (e.g. *Genoveva, Hoenapamea*) into the T-shaped vesica with several autapomorphic modifications in the monophyletic species groups. Marks of male interlocking structures (carina, subbasal and submedial cornuti, terminal diverticula) have been observed in female genitalia. These genera are mostly Holarctic with the exception of some few species occurring in montane insular areas of tropical (Indo-Malayan) SE Asia, e.g. Sri Lanka, New Guinea, Borneo, Philippines) and also in the Madagascarian area. They generally show a temperate-subtropical arboreal character despite of the fact that they are connected with herbaceous/grassy vegetation. There are some oreo-tundral species, mostly in the *A. zeta*-group, but only a few steppic species, e.g. *A. ferrago, A. leucodon*. Endemic species of *Apamea* and related genera are confined mostly to montane areas of SE Asia (e.g. Northern India, Nepal, Vietnam, Southern China, and Taiwan). Each of these areas exhibit more than 10 stenochorous species. The highest concentration of endemic species has been observed, however, in another Himalayan area. Nepal proved to be one of the most important centres of diversification of the whole subtribe Apameina. Some strictly localised taxa of Apameina, mostly of oligotypic genera and subgenera, have formed pairs of sibling species. These mono- or oligotypic subgenera or species groups of *Apamea* can be regularly characterised by well-defined genital structures (see: diagnoses of these genera, subgenera and species-groups). The expressed geographical and morphological gaps among these taxa strongly support our hypothesis that the main radiation of Apameina might have proceeded in the area between the southern Himalayas and SW China/Indochina.
In the taxonomic and biogeographical subdivision of *Apameina* and within the genus *Apamea* s. str. a characteristic SE vs. NW Palaearctic trend can be observed. In SE Asia there are numerous, mono- or oligotypic genera and species-groups, with striking genital differences and often curious autapomorphic characters combined with obviously plesiomorphic characters, e.g. the long, tubular vesica or the cucullus, more or less evenly covered by strong setae. Oppositely, the western Palaearctic and circumboreal/arctic species are often slightly differentiated with not very obvious genital differences, see, for instance, most species of the *A. monoglypha*- and *zeta*- species-groups. We can hypothesise that these trends are connected with the SE Asiatic (Kathaysian) origin of Apameina and the primary South-Himalayan diversification of this generic group, similarly to several genera of the SE Asiatic "winter fauna" of Noctuidae and Thyatiridae.

The genus ***Xenophysa*** Boursin, 1969 has been revised with the description of a new subgenus *Paraxenophysa*, with the description of a new species *Xenophysa pseudopoecila*, and with re-description of 4 species. The distribution and phylogeny of the genus was re-considered. *Xenophysa* s. str. was subdivided based on synapomorphic genital structures of both sexes into a Western and an Inner Asiatic clade.
Xenophysa species are generally rather uniform both in external characters and male genitalia. *Xenophysa* belongs to the 7th generic group of the Xestiina subtribus of Noctuini (Lafontaine, 1998) based on the following male genital characters: *(i)* Cucullus and corona reduced; *(ii)* valvae with small subapical digitus; *(iii)* vesica simple without sclerotised structures; *(iv)* antrum and ductus bursae strongly sclerotised. *Xenophysa* species can mostly compared with some smaller *Xestia*-related genera as *Estimata* Kozhanchikov, 1928 (*Rev. russ. ent.* **22**: 94), *Erebophasma* Boursin, 1963 (*Forsch. Ber. Land. Nordrhein-Westphalen* 1170: 73) and *Spinipalpa* Alphéraky, 1892 (*Horae Soc. ent. ross*. **26**: 444). Male genitalia show some very peculiar, mostly autapomorphic characters, similarly to the female genitalia which also display several remarkable characters. The tergite and sternite of the 9. segment are forming a sclerotised ring and the strongly sclerotised bilateral arms of the antrum are firmly attached to

this segment. Antrum has a U- or V-shaped incision which corresponds with the thicker or slender shape of the aedeagus.
Talk was presented at the IX European Congress of Entomology in Budapest (Abstract). Manuscript was submitted to *Zootaxa* (under revision).

The genus ***Rhyacia*** Hübner, [1821] 1816 belongs to the most heterogenous genera of the subfamily Noctuinae. Some species groups have numerous homologous structures, probably synapomorphies, with the species of genera *Epipsilia* Hübner, [1821] 1816 and *Chersotis* Boisduval, 1840. Both the external appeareance and the genital structures of the species and species-groups are highly characteristic, thus the species can be naturally grouped into species-groups. Certain species-groups consist only of a single or few species while others are more rich in species. Some of these species-groups can be characterised by the rather specialised "key" structures of the carina and by the corresponding "lock" structures of the strongly sclerotised antrum. Two of these subgenera will be discussed here with descriptions of new taxa and re-description of a subgenus with new taxonomical status.
The taxonomical evaluation of the genus *Standfussrhyacia* Hacker & Varga, 1990, erected for the species *Standfussrhyacia chimaera* Hacker & Varga, 1990, has been changed. It was suggested as the subgeneric name for all the species of the genus *Rhyacia* closely related with *Rhyacia junonia* (Staudinger, 1881). This change is a result of the description of several new *Rhyacia* species together with the taxonomic revision of the entire genus. *Rhyacia* was subdivided into 15 species groups which are merged into 6 subgenera, inter alia *Standfussrhyacia*. *Ancorhyacia* subgen. n. is described for the species groups 3.1.-3.3. with the type species *Rhyacia nyctimerides*. 3 new species are described from the high mountains of Central Asia: *Rhyacia unicornis* from Western China (Altyn-Tagh), *Rh. gyulaipeteri* and *Rh. horroreas* from North Pakistan (Karakoram Mts and Kashmir: W Himalaya).
Two publications will be submitted (*Acta Zool. Hung.*, *Zootaxa*).

Objectives and main achievements of the project

We planned to survey and answer some long disputed theoretical questions, as:

(i) Can we support the direct connection between the increase of the species numbers and the polyandry, and with the sperm competition; and
(ii) Can we detect the principle of parsimony in the morphological evolution of the copulatory organs?
(iii) Whether the similar functional constraints can lead to similar morphological solutions in the „lock-and-key" structures in phylogenetically distant groups, in which processes some basic biomechanical principles can be unravelled.

The questions 2. and 3. can be definitely answered based on our recent results, while the first one only partially. We collected a large number of data which support the earlier observations, but they are only partially evaluated.
The most diverse genera of higher ("trifid") Noctuidae are without exception polyandric. We collected data from about 650 species of 8 genera, belonging to 5 different subfamilies (Noctuinae, Hadeninae, Xyleninae, Heliothinae, Plusiinae). Mostly polyandric genera are: *Euxoa* (up to 5 spermatophores), *Orthosia* s.l. (with significant specific differences in the "female availability", with highest polyandry and fertility in *O. cruda*, lowest values at the „late spring" species, with shortest time of "female availability") and *Polia*. Not yet clarified, however, whether the high level of polyandry is characteristic for the "pest clade" of higher Noctuidae or for the whole family/superfamily.

We have shown the parsimony in male-female coevolutionary changes of genital structures. In several genera of Noctuinae (e.g. *Chersotis*) and Hadeninae (*Ctenoceratoda, Tricheurois*) the simplified genital capsula is combined with rather sophisticated spatial configuration of endophallus (vesica) with corresponding female ”lock” structures. Oppositely, simplification of endophallus is often connected with complex and/or dyssymmetric external genitalia (mostly saccular processes, see e.g. in the subtribe Discestriina of Hadeninae). We also demonstrated that similar trends of dyssymmetrisation often parallel occur in not closely related or even distant genera/subfamilies, e.g. in the subtribes Poliina and Discestrina of Hadeninae (Varga & Ronkay 2011) but connected with completely different trends in evolution of inner genitalia (endophallus vs. appendix bursae).
We have considered and discussed the external genital structures as correlated elements of a phylogenetically inherited “bauplan” in which some changes in details can be explained by selection due to optimalisation of the reproductive success (Varga & Ronkay 2011). The major pathways of change, however, are delimited by phyletic constraints which parallel appear in different phyletic lines of a major monophyletic group, i.e. the trifine Noctuidae.
One of these constraints is the stabilisation of symmetry in structures with own musculature. Oppositely, some rigid parts without own musculature can more rapidly and divergently evolve in which the different allocation of functions may have some selective advantages due to more effective stimulation, on one side, and fixation of genital parts during the elongate copulation, on the other. *Dyssymmetrisation can effectively enhance the variations of the spatial geometry of these “spandrels” but without the change of the “bauplan” which can be parallel preserved in different taxonomical groups.*
The Hadeninae subtribes Poliina and Discestrina display both individual and geographical variability in degree of dyssymmetrisation in several, widely distributed and morphologically mostly derived species, e.g. *Polia serratilinea* and *Hadula odontites*. Both species have a wide but disjunct distribution from Southern and Central Europe to Central Asia, with several described subspecies and subspecific differences in saccular processes (Varga & Ronkay 2011, see Figs 28 and 32).
In the most diverse genera of subfamily Noctuinae, *Euxoa* and *Agrotis*, the characters of the relatively simple male external genitalia often overlap in closely related species. We also have found that in these genera there are groups of sibling species in which even the endophallic structures probably cannot exclude the interspecific hybridisation, at least under experimental situations (Byers & Hinks 1978; Lafontaine 1981: 69). In these species groups *the different antennal structures can support the pre-copulatory isolation* and the *distinct anal papillae refer to the selection of different substrate for oviposition* (e.g. *Euxoa tritici*-group).
A further question was whether the morphological approach is proved to be useful in the survey of the origin and function of the signa. In quadrifine Noctuidae, e.g. Herminiinae varied forms of signa are often coupled with relatively simple forms of short vesica, often without sclerotised structures. Oppositely, signa in higher noctuid moths are relatively uniform, spot- or stripe-like structures. They are present with few exceptions in all trifine subfamilies, including Noctuinae. In Noctuini they are present practically in all genera (e.g. in *Xestia, Eugraphe, Eugnorisma* etc.), but they often disappear in diverse genera of Agrotina, (e.g. *Euxoa, Dichagyris, Agrotis*) in which also the sclerotised structures of vesica (cornuti) are weakly expressed, reduced or substituted by specialised scabrous surface structures.
We could not observe any direct morphological contact between sclerotised structures (cornuti, brushes of fasciculate cornuti) of vesica and signa in bursa. The latter are surely *not* fastening structures with carina and subbasal cornuti (see”structural” hypotheses of Hinton 1964 etc.). Oppositely, female genitalia regularly show co-adapted ”pouch-like” structures of ductus bursae or upper rugulose part of bursa for reception of huge subbasal or submedial cornuti (e.g. *Chersotis, Rhyacia, Eugnorisma, Apamea*), shown by us in recent (Zilli et al.

2009; Varga 2011a,b mscr.) and earlier publications. On the other hand, direct contact of long, tubular vesica fortified by a stripe fasciculate bristles (cornuti) with long, tubular appendix bursae was observed in many cases (*Ctenoceratoda, Sideridis, Harutaeographa, Perigrapha*, etc.). The hypothesis that signa are adaptations for better oviposition rate (Cordero 2005) can also be refused, since some genera of the ”pest clade” show a rather high fertility, e.g. *Agrotis, Euxoa* etc. *Signa never occur in appendix bursae*, i.e. near to the apertura of spermatophores, but only in corpus bursae, therefore *the spermatophore opening function can simply excluded*. The clarification of the digestive function, however, did not belong to the scope of our surveys and needs further studies. If it would be so, it could be a sign for sexual conflict, since female is interested in additional male supply while males are interested in fertilisation.
The origin and function of cornuti is also a disputed question. Based on our generic revisions we could establish some basic trends in the origin and evolution of cornuti. The separation of strong basal cornuti from the sclerotised carina can be regularly observed in phylogenetically not closely related groups, e.g. *Conisania, Hada, Lasianobia, Apamea.* These cornuti are often bulbed or sitting on a sclerotised plate but not attached to subbasal diverticula. Spine- or needle-shaped cornuti attached to subbasal diverticula and also the terminal, often fasciculate cornuti regularly occur in most subfamilies of trifine Noctuidae, thus they probably belong to the basic „architecture” of the inner genitalia of this group.

Additional results on modes and patterns of speciation in trifine Noctuidae

- We have recognised some elementary monophyletic units (species groups and higher level taxonomic categories) based on co-evolved homologous structures (monophyletic groups in *Chersotis, Rhyacia, Diarsia, Polymixis*, in the *Eugnorisma-Eugraphe* and the *Agrochola-Conistra* generic complexes, the entire tribe Cuculliini, etc). These groups will be considered in detail in the next volumes of the *Taxonomic Atlas of Eurasian and North African Noctuoidea* book series (Ronkay L. 2010, talk at the IX. European Congress of Entomology).
- In numerous cases the allopatric mechanism of speciation was proved. We established the allopatric ranges of members of monophyletic species groups (e.g. in *Dichagyris* and *Chersotis*) and outlined the areas of endemisms within these genera (Varga Z. 2009, Talk at the 16th European Congress of Lepidopterology). We could establish well-defined monophyletic species-groups by our taxonomic revisions in several diverse genera. These groups display such strictly correlative synapomorphies in the corresponding parts of the male and female genitalia which could only have been developed by co-evolutive processes, by optimalisation of the spermatophore transfer.
- The principle of homology was used in the identification and description of the basic genital structures of the „trifine” Noctuidae, focusing onto the following structures and processes (in the last period additionally surveyed also by scanning electron microscopy):
  (i) Correlative homologous structures as components of a supraspecific ”architecture” (e.g. in the *Chersotis-Rhyacia* monophylum and its species groups; Varga & Ronkay 2011; Varga 2011a,b mscr.).
  (ii) Translocation and fusion of homologous structures connected with functional changes (e.g. the modification and transformation of the clavus-juxta complex, with parallel functional solutions in different trifine Noctuidae groups; e.g. *Diarsia, Xestia, Agrochola, Amphipoea, Thysanoplusia, Ctenoplusia, Abrostola*, etc.); see: Varga & Ronkay 2011).

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Books (with acknowledgements on the support of OTKA)

ZILLI, A., **VARGA, Z.**, MIKKOLA, K., RONKAY, G. & **RONKAY, L.** (2009): *A Taxonomic Atlas of the Eurasian and North African Noctuoidea. Volume III. Apameini I.* – Heterocera Press, Budapest, ca. 350 pp, 57 colour plates and 156 genitalia plates.

FIBIGER, M., **RONKAY, L.,** YELA, J.L. & ZILLI, A. (2010): *Pantheinae-Bryophilinae. – Rivulinae – Phytometrinae, and Micronoctuidae, including Supplement to Noctuidae Europaeae, vols 1-11. Noctuidae Europaeae, volume 12.* – Entomological Press, Sorø, 504 pp. + 13 colour plates.

Book (published in the reporting period, but unfortunately without acknowledgements)

RONKAY, G. & **RONKAY, L.** (2009): *A Taxonomic Atlas of the Eurasian and North African Noctuoidea. Volume II. Cuculliinae I.* – Heterocera Press, Budapest, 365 pp, 57 colour plates and 150 genitalia plates.

Publications in international journals and book series

RONKAY, G., **RONKAY, L.,** GYULAI, P. & HACKER, H. (2010): New Psaphidinae and Oncocnemidinae (Lepidoptera, Noctuidae) species and genera from the wide sense Himalayan region. – *Esperiana* **15**: 223-244; plates 30-33.

RONKAY, G., **RONKAY, L.,** GYULAI, P. & HACKER, H. (2010): New Orthosiini (Lepidoptera, Noctuidae, Hadeninae) species and genera from the wide sense Himalayan region. – *Esperiana* **15**: 127-221; plates 12-29.

RONKAY, G., **RONKAY, L**., GYULAI, P. & HACKER, H. (2010): New Xylenini (Lepidoptera, Noctuidae, Hadeninae) species and genera from the wide sense Himalayan region. – *Esperiana* **15**: 245-358; plates 34-54.

VARGA, Z. (2010): Biogeography of West Palaearctic Noctuidae. In: Fibiger, M., Ronkay, L., Yela, J.L. & Zilli, A.: *Noctuidae Europaeae* 12 (incl. Suppl. 1-12), pp. 265-274. Entomological Press, Sorø.

Submitted publications (under revision)

VARGA, Z. (2011) Revision of the genus *Xenophysa* Boursin, 1969 (Lepidoptera, Noctuidae) Submitted to *Zootaxa*

VARGA, Z. & RONKAY, L. (2011) Architecture, simple physical principles, functional differentiation and dyssymmetry in male external genitalia in Noctuidae (Lepidoptera) Submitted to *European Journal of Entomology*

Talks at international conferences

MIKKOLA, K., RONKAY, G., **RONKAY, L**., **VARGA, Z.** & ZILLI, A. (2009): The revision of the Apamea generic complex (Noctuidae). I. The ancient groups of the Himalayan-Sino-Pacific Apamea s.l. – 16th European Congress of Lepidopterology, Cluj-Napoca/ Kolozsvár, 25-28. May 2009.

RONKAY, G. & **RONKAY, L**. (2009): New results in the taxonomy of the genus Cucullia sensu lato (Noctuidae). – 16th European Congress of Lepidopterology, Cluj-Napoca/ Kolozsvár, 25-28. May 2009.

VARGA, Z. (2009): Trends and biomechanical constraints in the structure and function of genitalia: contribution to the „lock-and-key principle (Noctuidae: Noctuinae, Hadeninae). – 16th European Congress of Lepidopterology, Cluj-Napoca/Kolozsvár, 25-28. May 2009.

RONKAY, L. (2010): The Taxonomic Atlas – lessons and perspectives. IX. European Congress of Entomology, Budapest, 22-27. August 2010.

VARGA, Z. (2010): Revision of the genus Xenophysa. IX. European Congress of Entomology, Budapest, 22-27. August 2010.

Manuscripts ready for submission

VARGA, Z. (2011): Revision of the genus *Rhyacia* Hübner, [1821] I: The *Rhyacia junonia* species group with re-description of the subgenus *Standfussrhyacia* Hacker & Varga, 1990 (stat. nov.), with description of the new subgenus *Anchorhyacia* and three new species, – To submit: *Acta Zoologica Acad. Sci. Hung*.

VARGA, Z. (2011): Revision of the genus *Chersotis* Boisduval, 1840 I: Species groups, new and revised species of the genus. – To submit: *Zootaxa.*

Electronic documentation

All publications (books, papers, talks) are electronically documented with a high number of digital photographs of specimens (holo- and paratypes of surveyed taxa) and genital slides. These specimens and microscopic preparates are preserved in several large public collections, mostly (more than 15 000 slides) in the Hungarian Natural History Museum and at the Scientific Collection of the Evolutionary Zoology Department of the University of Debrecen, but also in large European Museums. The slides and documentation of the materials from the latter institutions are produced, of course, not exclusively by the senior researchers, but also by some colleagues whose names are mentioned in the publications (G. Behounek, P. Gyulai, V. Kononenko, W. Speidel, G. Ronkay, A. Zilli).

Appendix

The preparation of this final report was hindered by some unfortunate circumstances. The senior researcher, Dr. László Ronkay was moved at December 2009 from the Lepidoptera Collection of the Museum and transfered to an other department of the Museum, despite of the protest of several internationally ackowledged experts. This treat has resulted in several unadvantageous consequences. E.g. the even the principal applicant could regain some materials for survey with a considerable delay which were temporarily deposited in the Museum for joint surveys and publications with Dr. Ronkay.